12-1949

The Species Concept: A Semantic Review

Benjamin H. Burma
University of Nebraska-Lincoln

THE SPECIES CONCEPT: A DISCUSSION

THE SPECIES CONCEPT: A SEMANTIC REVIEW

BENJAMIN H. BURMA
Department of Geology, University of Nebraska, Lincoln

Received February 10, 1949

In some respects, it is extremely unfortunate that names are ever attached either to ideas or objects. The false attachment of names to ideas or objects similar but not identical with the original can work harm far exceeding the benefits conferred by having a convenient label. The name "species" has come to such a state.

As we shall see, a species, be it plant or animal, is a fiction, a mental construct without objective existence. Animal, and plant, lines of descent exist in a four-dimensional continuum. To set up species in this continuous line of descent, we must chop it into units, and in any such process the divisions are purely arbitrary. Available information makes such a view more or less self-evident. What, then, is a "species"? Instead of starting with an evolutionary line and dealing with it on the basis of preconceived concepts, working from the top down, so to speak, let us work from the bottom up.

Our starting point will be an individual animal, which for convenience we will say answers to the name of John. John is a sexually-reproducing animal. As such, he comes into existence at the moment that certain sperm and egg nuclei fuse, at which moment we may refer to him as $John_0$, one cell with a nucleus. The next time we look for $John_0$, we can't find him. In his place, we find a stranger with two cells. Ah-ha, we say, John has undergone cell-division. We are confident that if we had observed $John_0$ we would have seen his continuous transformation into this two-celled stranger who is obviously *not* $John_0$. Since we are sure he does have some sort of a very close relation to $John_0$, we decide to call this new animal $John_1$. Similarly we find $John_1$ displaced by $John_2$ and he by $John_{3, 4, 5, \ldots n}$. Thus we have followed what is usually called the "growing-up," or the ontogeny of an individual. But *what* is John? Obviously, he is not the same thing at any two successive instants. Now he is $John_{1324}$; the next instant he is $John_{1325}$, forever and irrevocably different from any John that has come before or from any that will come in the future. Thus John is a succession of conformations of matter in time, and any meaningful study of him will have to consider the four-dimensional $John_{0+1+2+3+4+ \ldots n}$.

One fine spring day the tender passion stirs $John_n$'s breast, and he looks around for a mate. Within his immediate horizon he espies $Jane_{n+1}$, $Joan_{n+2}$ and $June_{n+3}$. For reasons too devious to explore at this time, $John_{n+4}$ chooses $Jane_{n+5}$ for his mate, or perhaps, *vice-versa*. Thus we pass from the individual to the breeding population, our next meaningful unit.

What precisely is a breeding population? From John's point of view, it includes all females with whom he might ordinarily mate; in other words, it takes in a territory extending from a central point out to the limits of John's wanderings. Such a territory includes males who would be equally glad to mate with the females of this same area. The total population of males and females ready, willing, and able to interbreed and centered around a particular animal we may denote a breeding population. Each individual in this population will also be the center of another breeding population, most of which will have territories extending beyond the original one. The character of a given breeding population is never identical at any two moments.

The individuals in it are constantly changing in character. New animals are constantly added by birth and immigration and others are lost by death and emigration. Furthermore, as the central animal travels, his breeding population shifts also in geographic position, adding and subtracting animals from the population in so doing.

Since we have defined the breeding population as comprising those females with which John will mate (or would if he had time and opportunity) and the males which can mate with them, it follows that the breeding population is characterized by a genetical continuity and similarity, fluid and shifting, but unmistakable. Naturally, the elements of this population will not be genetically identical, even apart from sex differences. No natural population is. But the germ plasms of $John_n$ and $Jane_n$ and/or $Joan_n$ and/or $June_n$ are similar and compatible at least to the extent that they produce viable and fertile offspring, thus insuring the continuity of the population. Thus we have a moderately definable, natural, biological unit composed of animals which in nature will interbreed as the opportunity presents.

From John to Jane to breeding population we have a certain biological continuum, the individuals of the breeding population being connected, figuratively, by strands of germ plasm which represent this continuity. When we try to deal with larger aggregates of individuals, our categories become more and more abstract and empty of any real meaning. Our basic taxonomic unit is, of course, the subspecies. The best description available of a subspecies seems to be that it is a geographically (or ecologically) isolated subdivision of a species. This says little enough. From our point of view, a subspecies would be a geographically confined aggregate of breeding populations.

What, then, is a species? It would seem thus far to be the whole of any one series of breeding populations. This is certainly an innocuous-seeming definition, but is it? The definition as it stands unfortunately puts all living and fossil animals in one species, since there is a continuity of germ-plasm back from John to the original primordial cell, and from it forward to every living animal (not to mention plant). Thus, if we ignore time, we end up with only one species, which is all to the good insofar as it emphasizes the unity of life and the Brotherhood of Man, but is of little use to the practicing taxonomist.

Can we avoid the temporal difficulty? Let us redefine the species as the whole of any one series of breeding populations *as it exists at any one time.* This definition merely lands us in an exactly opposite difficulty, for we now have an infinity of species, time being infinitely divisible. Both these definitions of species at least have the advantage of being as objective as possible, but if we try to keep the definition of a species objective and still useful, we are forced to bring into the definition a discrete unit of time. As soon as we do this, we are, of course, being arbitrary, and perhaps not a little ridiculous. If we *should* define a species as the whole of any one series of breeding populations in existence over a period of 10,000 years, who is to say as to when the year zero is to be? Further, insofar as paleontology is concerned, no absolute time scale of usable "fineness" and precision is obtainable, and no cognizance is taken of differing evolutionary rates.

Thus, we come back to our original contention, that "species" have only a subjective existence. Our real biological unit is the breeding population, since it is through this ever-changing unit that the germ-plasm is passed. Taxonomy takes no notice of the breeding population, but any permanently useful taxonomic system must take account of its existence and its significance. Species and subspecies are the units with which the taxonomist deals, but they are merely convenient labels for arbitrary groupings and have only a minimum of biological meaning.

THE SPECIES CONCEPT: SEMANTICS VERSUS SEMANTICS

ERNST MAYR
The American Museum of Natural History, New York

Received June 24, 1949

The question whether or not species have objective reality is a perennial one. If a species were merely "a fiction, a mental construct without objective existence" one would expect under all circumstances the borderline between species to be exceedingly vague and subjective. However, if Dr. Burma should make an excursion into the neighborhood of his home town, he will find that every species of birds and mammals is sharply separated from every other one. This is not an exceptional situation; in fact it is the condition naturalists find in every part of the world. The primitive Papuan of the mountains of New Guinea recognizes as species exactly the same natural units that are called species by the museum ornithologist (Mayr, 1946). The arrangement of organic life into well-defined units is universal, and it is this striking discontinuity between local populations which impressed the naturalists Ray and Linnaeus and led to the development of the species concept. There can be no argument as to the objective reality of the gaps between local species in sexually reproducing organisms.

An excursion into the field of semantics appears helpful at this point. There are concepts that are absolute, like stone or fire, and others that are relative. If I meet an unknown man I do not know whether or not he is a brother. He is a brother only in relation to another person (a brother or sister of his). The word species likewise is such a relational term. It separates interbreeding populations from all others. In fact, the word species is most meaningful in connection with populations that are *not* conspecific, populations that are separated by a reproductive gap.

It has been pointed out (Burma, above) that it is virtually impossible to delimit a breeding population. Though many individuals are obviously members of a single effective, local breeding population, there are other individuals, more distant in space and time, which might possibly belong to different populations of the same species. It is not possible to undertake a clearcut delimitation of one breeding population of a species against others. This is no major tragedy at this point since we are not discussing the delimitation of breeding populations. What is important is the fact that there is *no* difficulty in delimiting a breeding population of one species against a sympatric-synchronous breeding population of other species. The gap between such species is well defined and has objective reality.

The presence or absence of a reproductive gap can be tested only where populations are in contact. The species thus has full objective reality only in a local fauna or flora. This *non-dimensional species* (Mayr, l.c.) is the standard of the species concept as originally conceived by Ray and Linnaeus. The objective reality of *this* species is beyond doubt.

To repeat once more, the essence of the species concept is the non-interbreeding of a population with other populations, a phenomenon which can be tested only where such populations are in contact. No matter how different certain individuals might be (polymorphs, larval stages, etc.), as soon as it is established that they are members of a single breeding population, they are considered conspecific.

The difficulties which Dr. Burma sees are not those of the original, non-dimensional species concept. Rather they are due to an expansion of this species concept in space and time. All species are subject to evolutionary change since, as Dobzhansky stated so truly, the species is merely a stage in an evolutionary process.

It is implicit in the theory of evolution that species should change in space and in time. There should be populations in an evolutionary series which are on the borderline between an ancestral and a daughter species. But even such a borderline population is as good a species in relation to others *with which it is in contact* as any normal species.

The difficulties to the practical application of the species concept caused by evolution are more apparent than real. There are gaps even in a multidimensional system. These gaps, as far as paleontologists are concerned, are caused by the extreme scantiness of the fossil record. The number of well described transformations of one species into another one is actually very small. Usually there is either a sequence of sharply discontinuous species as with the Eocene oysters of Texas (Stenzel, 1949) or else the sequence consists of slight subspecies, with even the extremes not yet having reached full species level. The fact that species are the product of evolution and continue to evolve seems only rarely to become a source of practical difficulties for paleontologists. In the majority of the cases the working paleontologist is dealing with a non-dimensional situation (as described above). In a single horizon at a single locality the species of the paleontologist are as well defined as are those of the local naturalist. Whenever a paleontologist runs into difficulties in such a non-dimensional system, it is not due to the weakness of the species concept but rather due to difficulties of taxonomic analysis (polymorphism, ecophenotypes, age variation, etc.).

The species concept has not only its greatest objective reality in a non-dimensional system, but also its greatest usefulness. In a sympatric-synchronous situation there is nothing intermediate between breeding populations and species. If a paleontologist studies a series of specimens from a given horizon, he knows that they are all either members of a single species or of different species. By definition there can be no intermediate stages in such a collection as, for example, subspecies. The species concept not only permits but actually demands an unequivocal decision. The species to be delimited in such cases by the practical taxonomist is by no means "a mental construct without objective existence," as claimed by Dr. Burma.

In all multidimensional situations an inference has to be made (Simpson, 1943) on the basis of the objective species of the non-dimensional system. The subjectivity of this expanded species concept by no means invalidates the species concept *per se*. The species of the local naturalist or of the paleontologist within a given horizon is clearly delimited against other species and can thus be considered as having objective reality.

Literature Cited

Mayr, E. 1946. The naturalist in Leidy's time and today. Proc. Acad. Nat. Sci. Philadelphia, **98**: 271–276.

Simpson, G. G. 1943. Criteria for genera, species, and subspecies in zoology and paleozoology. Annals of N. Y. Acad. Sci., **44**: 145–178.

Stenzel, H. B. 1949. Successional speciation in paleontology: the case of the oysters of the *sellaeformis* stock. Evolution, **3**: 34–50.

POSTSCRIPTUM

Benjamin H. Burma

At first glance it will seem that Dr. Mayr and I are indeed far apart in our conception of species. However, I believe that a close reading will show that our positions are actually not so very different after all. The neozoologist is usually impressed by the distinctness of the "species" he sees in the world today. On the other hand, the paleontologist is more likely to be impressed by the continuity of a given evolutionary line. Dr. Mayr's criticisms, I believe, do not actu-

ally attack the fundamental basis of my argument, the complete subjectivity of the concept of "species" when viewed in a four-dimensional space-time rather than in the unreal three-dimensional space of static time. They do focus attention on the practical utility of species as used by the neozoologist.

I cannot, however, agree that paleontologists are so uniformly impressed by the objective reality of species. It is true that in the past paleontologists seemed to have been little troubled by this. On the other hand, it is well to remember that many of the paleontologic species of fifty years ago are the genera and subgenera of today. The paleontologist of today finds it more and more difficult to recognize valid differences between the "species" of a given phyletic line as collecting and study become more thorough. It is this practical and growing difficulty which prompted my foregoing analysis of the species concept.